#1574

Is Heterobasidion annosum poorly adapted to incite disease in cool, wet environments?

Charles G. Shaw, III, USDA Forest Service,
Rocky Mountain Forest and Range Experiment Station,
240 West Prospect, Fort Collins Co 80524.

ABSTRACT

An argument is advanced to suggest that infection, survival, and damage caused by Heterobasidion annosum is markedly less under cool, wet conditions than in other climates. This premise is supported by the author's imagination, experience in southeast Alaska, and data from this area and other sources. In general, a cool, wet environment reduces the airborne population of spores and washes many of them from stump surfaces. Evaporation of water from stump surfaces also is reduced which helps to maintain a high moisture content in stumps. This condition likely reduces the availability of oxygen which inhibits infection by, and survival of, H. annosum in stumps. In contrast, primarily saprophytic Armillaria spp. survive under these same conditions and through rather rapid colonization of stump and root wood limit the opportunity for whatever H. annosum does become established to spread and incite disease in surrounding trees.

INTRODUCTION

Heterobasidion annosum (Fr.) Karst. damages numerous coniferous species growing under various, primarily temperate, environmental conditions in many localities around the world (Pegler and Waterson 1968). It is, however, this paper's purposely provocative premise that damage from this organism is markedly less in cool, wet environs than in those characterized by either warm and wet (i.e., southeastern United States), warm and dry (i.e., south-central Oregon and the east side of the Serria Nevada mountains), or cool and dry climates (i.e., interior Scandinavia).

I developed this hypothesis after years of often shivering and sopping-wet fieldwork in southeast Alaska revealed limited infection by, and survival of, H. annosum in stumps of Sitka spruce (Picea stichensis (Bong.) Carr.) and western hemlock (Tsuga heterophylla (Raf.) Sarg.)--let alone any damage in standing trees (Shaw 1989). Additional data to support the hypothesis were selectively drawn from other sources.

The Situation in Southeast Alaska Over 120,000 ha of old growth Sitka spruce/western hemlock forest have been harvested through clearcutting on the mainlands and islands of southeast Alaska (Harris and Farr 1974). Young stands of these species have regenerated naturally into the cut areas with generally adequate stocking and vigorous growth (Harris 1974). At age 15-20, many of these stands are precommercially thinned--an operation that creates numerous stumps that may serve as infection courts for root disease fungi.

Spores of H. annosum and Armillaria spp. are relatively common in these young stands even though basidiocarps of H. annosum are rare (Shaw 1981a,b), as is infection of large and small stumps of both species (Shaw 1981a, 1985, 1989, Tait et al. 1985). In contrast, stump colonization by Armillaria spp., probably by contact of its roots with rhizomorphs or infected roots rather than

by spores (Wargo and Shaw 1985), is considerably more frequent (Shaw 1981a, 1985, 1989, Tait et al. 1985), but death of surrounding trees is still infrequent.

But and stem decay are common in old-growth trees in the area where gross timber volumes in affected stands have often been reduced by one-third of more (Farr et al. 1976) through rot caused primarily by hymenomycetes--H. annosum, Armillaria spp. and Phaeolus schweinitzii (Fr.) Pat (Kimmy, 1956). Even in these old-growth forests, however, sporophores of H. annosum are rare, as Kimmy noted on a herbarium collection form filed at the Forestry Sciences Laboratory in Juneau, Alaska. In addition, T. Laurent (personal communication) found no basidiocarps of H. annosum, although its decay was common, when he dissected 1776 trees to measure cull at 67 locations in southeast Alaska (Farr et al. 1976). Several basidiocarps previously collected in southeast Alaska and identified as H. annosum (Cooke 1955, Cooke and Shaw 1952) have been reexamined and found to be Fomitopsis pinicola (Swartz:Fr.) Karst (R. Gilbertson personal communication). During 9 years of collecting in southeast Alaska, I gathered basidiocarps of H. annosum only once (Shaw and Florance 1979) and bribed students found none. Thus, the source of spores for the airborne inoculum that does exist (Shaw 1981a,b) remains an enigma.

As indicated, several studies in southeast Alaska found limited stump colonization by H. annosum--an event considered to be a necessary precursor to development of damaging disease levels in managed, young stands of Sitka spruce and western hemlock. Because of this situation, I recently concluded (Shaw 1989) that in southeast Alaska there was little likelihood that H. annosum would damage young, managed stands of Sitka spruce and western hemlock within the planned 90 to 120 year rotation. The questions still remains, however, why not??

Environmental Condition of Stumps My data (Shaw 1981a, 1985, 1989) and Morrison's (1976, Morrison et al. 1986) indicate that H. annosum becomes a less common inhabitant of thinning stumps with movement north along the west coast of North America. With movement north, lower temperatures (Farr and Harris 1979) and higher precipitation (Farr and Hard 1987) probably reduce the aerial spore population of H. annosum (Reynolds and Wallis 1966) and wash many spores from stump surfaces. Also, Redfern (1982) suggests from locations in Scotland near the latitude of southeast Alaska, that infection of Sitka spruce stumps may be limited by high rainfall, and that on sites with high rainfall, H. annosum is absent from stumps with a high moisture content. These result are similar to those found in southeast Alaska (Shaw 1989) where rain is common on any date (Farr and Hard 1987, NOOA 1978) and where moisture contents of Sitka spruce and western hemlock stumps are often well over 100% (Shaw 1989).

Perhaps the high moisture content of these stumps reduces availability of O_2 to a level that inhibits growth of H. annosum--a reason suggested for the lack of growth by H. annosum in white fir wetwood (Worrall and Parmeter 1983). The low temperatures common to southeast Alaska could further affect fungal utilization of the limited O_2 available as they would lower overall metabolic rates and inhibit evaporation of water from stumps surfaces.

In vitro studies indicate that H. annosum (Worrall and Parmeter 1983), Armillaria spp. (Smith and Griffin 1971, Worrall et al. 1986), and an array of other wood decay fungi (Jensen 1967, Scheffer 1986, Worrall and Parmeter 1983) can grow at extremely low levels of available O_2. Extrapolation of these in vitro results to decay of stumps in situ is, however, difficult as the availability of O_2 in woody substrates is complicated by distribution patterns of water and air in cell walls and pores, and effects on this

distribution by decay, moisture content, temperature, and other microenvironmental conditions (Boddy 1983).

The moisture content of wood at which no air spaces would remain can be calculated if the specific gravity (SG) of the species in question and that of solid wood substance are known. I made such calculations, using 1.5 for the SG of solid wood substance, a value that is rather constant regardless of tree species (Wangaard 1950), and a range of values between 0.34 and 0.44 for the SG of wood from Sitka spruce and western hemlock, values determined for young trees of these species in southeast Alaska (Farr 1973). These calculations indicate that at a moisture content between 161% and 227% (depending on SG) all pore spaces in these woods would be water-filled and thus unavailable for air; values comparable to those found in many stumps from southeast Alaska (Shaw 1989).

In vitro studies indicate that decay by certain fungi is inhibited in Sitka spruce wood at moisture contents around 150% and that decay stops near 190% (Boyce 1961); a value within the above-calculated theoretical range for all available pore spaces to be water-filled. Redfern (1989) suggests that at saturation levels somewhat above 70%, Sitka spruce wood is unsuitable for growth of H. annosum. Using a SG of 0.36, this 70% saturation level corresponds to a moisture content of 147%, a value that many of the stumps from southeast Alaska, particularly Sitka spruce, exceeded (Shaw 1989). Even though H. annosum frequently failed to colonize stumps in southeast Alaska with a moisture content below that necessary for total occupancy of the pore spaces by water, these calculations appear to support the contention that O_2 availability may limit colonization of wet, cool stumps by H. annosum.

Growth of Armillaria may also be reduced at extremely low levels of available O_2 (Smith and Griffin 1971, Worrall et al. 1986); however, three features of stump colonization by this fungus, in contrast to that by H. annosum, could allow Armillaria spp. to survive in O_2-poor stump wood:

1) Typically, H. annosum initially colonizes more interior portions of stumps while Armillaria initiates colonization between the bark and wood where more air should to be present.

2) Rhizomorphs of Armillaria spp., which are common on interior surfaces of bark on these stumps and in the surrounding soil, can absorb O_2 at their growing tips (Smith and Griffin 1971). Although it is unclear how far back down the rhizomorph such absorbed O_2 might be utilized, certain ions can be transported basispetally within rhizomorphs (Granlund et al 1985, Morrison 1975). Morrison (1976) also suggested that when Armillaria was growing from woody blocks with a high moisture content(170%), thus having a limited supply of O_2 available in the food base, the O_2 requirement for fungal growth was met by absorption from the soil atmosphere. Depending on the effective distance of O_2 transport down the rhizomorph, this mechanism may allow for growth of mycelium that is located in an O_2 poor environment.

3) Growth of Armillaria may be stimulated, even at low levels of O_2 (Worrall et al. 1986), by ethanol (Weinhold and Garroway 1966), a by-product of metabolism in Armillaria spp. (Tarry 1968) and other common soil microorganisms often associated with Armillaria spp.

The frequent occurrence of Armillaria spp. in stumps from southeast Alaska agrees with data from northern British Columbia (Morrison et al 1986) where 32% of the non-pine stumps were infected with an Armillaria sp. identified as North American Biological Species (NABS) V (Anderson and Ullrich 1979). The NABS of Armillaria spp. in stumps from southeast Alaska is poorly understood, but NABS V and IX are common in the region (Shaw and Loopstr 1988). Because these two species have limited pathogenic capabilities on coastal species and sites

(Morrison et al. 1985, Shaw and Loopstra 1988, Wargo and Shaw 1985) their common occupancy of stump wood may deter spread of the limited H. annosum that does inhabit stumps rather than act as an incitant of disease (Greig 1962, Morrison and Johnson 1978, Shaw 1981a, 1989).

What's It All Mean? Even though some might consider these rash ramblings representative of the worst in data free analysis, I challange those active in research on H. annosum to critically evaluate the following scenario, find the researchable topics, and go at it: Heterobasidion annosum is markedly less able to incite disease in managed, young stands growing under cool, wet conditions than in other climates. This situation develops because a cool, wet environment reduces the airborne population of spores and many of those that are deposited on stump surfaces wash away. In addition, evaporation of water from stump surfaces is reduced which helps to maintain a high moisture content in stumps. This condition reduces the availability of oxygen which inhibits infection by, and survival of, H. annosum in stumps. Low temperatures also affect utilization by H. annosum of the limited O_2 that is available as they lower overall metabolic rates. In contrast, primarily saprophytic Armillaria spp. survive under these same conditions and through rather rapid colonization of stump and root wood limit the opportunity for whatever H. annosum does become established to spread and incite disease in surrounding trees.

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